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Social Behavior and the Ontogeny of Foraging in the Kea (*Nestor notabilis*)

JUDY DIAMOND & ALAN B. BOND

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Abstract

Kea are omnivorous parrots endemic to the high mountains of the South Island of New Zealand. Over a two-year period, we recorded quantitative behavioral data from 38 banded male kea foraging at a refuse dump outside Arthur's Pass National Park and analyzed the effects of social factors on the ontogeny of foraging. Members of the four distinguishable age classes — fledglings, juveniles, subadults, and adults — displayed characteristic differences in foraging ability and in the social behavior used to obtain access to resources. Adults performed most of the excavation that uncovered new food resources. Fledglings explored and manipulated objects almost continuously, but they discovered little food on their own and were commonly fed directly by adults. Juveniles obtained the highest foraging yields for the amount of time spent searching of any age class, aided by appeasement behavior that gave them preferential access to foods discovered by adults. Kleptoparasitism served as a primary foraging strategy for subadults, who were otherwise poor at discovering and retaining food resources. Social factors influence the acquisition of foraging expertise in the Kea in different ways at different stages of development.

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Introduction

Kea are large, olive-green parrots that are endemic to alpine scrub and mountain beech forests on the South Island of New Zealand. Kea are known for their complex social behavior, omnivory, and destructiveness around human settlements (FORSHAW 1977). We examine the relationship between the social behavior of kea and the course of development of foraging skills in the young.

Young birds, in general, derive a variety of benefits from foraging in conspecific groups, including protection from predators (RUBENSTEIN 1978; HEINSOHN 1987) and opportunities to be fed by other members of the group (DRURY & SMITH 1968; BALDA & BALDA 1978; BROWN 1987; SNYDER et al. 1987). The most conspicuous potential benefit of group foraging, however, is that the behavior of experienced birds should provide reliable information about the location and appearance of high quality resources (KLOPFER 1959; TURNER 1965; TOLMAN 1968; CLAYTON 1978; GOCHFELD & BURGER

1982; JOHNSON 1986). Evidence also suggests that naive birds can acquire foraging techniques by observing the behavior of more experienced individuals (PALAMETA & LEFEBVRE 1985; LEFEBVRE 1986; SHERRY & GALEF 1990). The relationship between social factors and the ontogeny of foraging has seldom, however, been directly assessed in the field.

Several characteristics make kea ideal subjects for such a study. There is a long history of debate concerning the social transmission of foraging skills in the kea, particularly with regards to their proclivity for feeding on sheep (MARRINER 1908; BULLER 1967). More recently, CAMPBELL (1976) asserted that juvenile kea gain experience in different feeding methods by observing the activities of their peers, and BREJAART (1988) observed fledgling kea to follow adults who were feeding, and on various occasions, to pick up foods that were sampled or discarded by adults.

Studies on captive kea demonstrated age-related differences in foraging ability for at least two months after fledging (ZEIGLER 1975). The young develop slowly, fledging at between 9 and 13 weeks of age, with an extended post-fledging period of dependency on the parents (PORTER 1947; LINT 1958; JACKSON 1963; SCHMIDT 1971). They subsequently pass through a series of distinctive juvenile stages (SCHMIDT 1971). Male kea do not attain sexual maturity until at least their fourth or fifth year (MALLET 1973). In addition, kea are ecological generalists, feeding on over a hundred different species of plants and animals (CLARK 1970). They aggregate in large groups wherever food is abundant (CLARK 1970), providing young birds with extensive opportunities for social interaction. Together, these factors suggest a complex ontogeny, requiring extensive learning about both the social and the ecological environment.

Methods

Study Site

The study was conducted at a refuse dump in Arthur's Pass National Park on the South Island of New Zealand. The site is located south of Arthur's Pass Village on the Beady River at an elevation of 700 m, in an area surrounded by southern beech trees (*Nothofagus* sp.). The dump has existed at its present location for many years; according to JACKSON (1962), kea have foraged at this site since 1956.

Subjects and Sampling

Kea were captured with a manually operated drop-net and were banded with numbered monel metal bands and colored plastic bands to allow recognition of individuals at a distance. They were measured and weighed, and their sex and age class was determined. Females can be distinguished from males on the basis of bill length and overall size (BOND et al. 1991). Females are much less common than males in foraging aggregations, constituting less than 10% of the individuals present at any one time, and their behavior is strikingly different from that of males. Consequently, females were not included in this study, either as focal individuals or as participants in social interactions. Sex differences in foraging behavior will be addressed in a separate publication.

Ages were determined from visual markings. Four age classes are distinguishable in kea (LINT 1958; SCHMIDT 1971; KELLER 1972; MALLET 1973). Fledglings, in the summer of their emergence from the nest, have a bright yellow-orange eye ring, cere and mandible, and a light yellow cast to the crown feathers. Juveniles, which are birds in their second summer, have a pale yellow eye ring, cere, and lower mandible, but no yellow crown. Subadults, which are birds in

their third or fourth summer, retain an incomplete yellow eye ring, but have a dark cere and bill. In adults, the eye ring, cere, and bill are all dark brown.

On the basis of 250 instantaneous censuses of marked and unmarked animals during peak activity times, we were able to derive estimates of the number of animals in each age group in the local population (based on the Bailey modification of the Lincoln Index, BEGON 1979). A disproportionately large number of the birds were adult males, which is typical for foraging aggregations of kea (BELCHAM 1988). To maximize the validity of our comparisons, our sample of focal individuals was biased toward including larger numbers of young birds. In all, we recorded the behavior of 38 banded male kea: 17 adults, 8 subadults, 10 juveniles, and 3 fledglings.

Data collected in this study were obtained during 300 h of observation made over two field seasons: Nov. 19 to Dec. 9, 1988, and Jan. 7 to 27, 1990. The ethogram was formulated during a pilot study conducted between Dec. 13, 1986, and Jan. 3, 1987. Data were gathered in 10-min sessions, using focal-individual sampling, with six sessions being recorded from each animal. A bird was selected for recording only if it was already foraging or beginning to forage on the dump. Sessions that terminated prematurely, because the animal left the study area, were retained only if they were at least 7 min in length. No individual was recorded more than once in any 1-h period.

Recording Technique

A comprehensive ethogram for the species, including 82 behavior categories, was prepared from observations conducted during our pilot study and from comparisons to work done on captive individuals (POTTS 1969, 1976, 1977; KELLER 1975, 1976; ZEIGLER 1975; DIAMOND & BOND 1989). For recording purposes, this preliminary version was condensed to 39 behavioral categories, including 17 object-related categories and 22 social and other categories. Our categories of object-related behavior, including all foraging behavior, are described in an Appendix.

Social, locomotory, and maintenance behavior was generally recorded as composite categories that included several distinct action patterns. For example, we lumped as Attack the full repertoire of contact aggressive behavior described in POTTS (1969) and KELLER (1976). We used Threaten to refer to any of the noncontact aggressive displays. Similarly, the action patterns used in maintenance, reviewed in POTTS (1976), were aggregated into a Comfort category.

We also modified POTTS' (1969) description of the Hunch display. He described this as a posture in which the head and bill are directed downward and the body inclined forward, similar to what has been termed Bowing in other parrots (SMITH 1975). POTTS (1969) stated that the rump feathers are characteristically fluffed and the tail fanned out, while the humeri are held slightly out and upward from the body, and the forewings are drooped. From our observations, however, hunching may involve a range of additional features, as well, including head ruffling, body ruffling, bill gaping, vocalizing, and fanning the wings downward along the sides of the body.

Using a Toshiba 1100+ computer and KBDAC, a custom-designed, keyboard-based data-acquisition program, we generated a continuous record of the behavior of the focal animal and the time intervals between successive acts. When the focal individual engaged in social interactions, we recorded the age and sex of the interacting animal, as well as all behavior produced by both participants.

Data Extraction and Analysis

Three separate data sets were extracted from the transcripts of the observation sessions. In the first, the frequencies of all behavioral categories produced by the focal individual were obtained from each session. These were adjusted for time out of view to obtain frequencies per standardized 10-min session. The mean frequency across sessions was then computed for each

bird, generating a data set with one measure for each of the 39 categories for each focal individual.

The effects of age class on frequency were assessed with analysis of variance. For contrasts among the three older age classes, we used a two-way design (age x year) to remove the effects of differences between the two field seasons and general linear modeling (SAS 1985) to compensate for the unequal numbers of subjects per cell. Because fledglings were observed only in the 1989–90 field season, we used a one-way design, including just the observations from that season, for contrasts involving fledglings. For all cases in which there was a significant effect of age class, we subsequently performed simple comparisons to locate the source of the effect (KEPPEL 1982).

For the second data set, we derived activity budgets from the session transcripts by subdividing the sequences of behavioral events into bouts of 9 general classes of activity: Excavate, Search, Eat, Demolish, Transport, Social, Scrape, Glean, and Maintain. The beginning and ending of each bout was defined objectively by means of a consistency table: For each activity class, each behavior was defined as being either characteristic of the activity, consistent with the activity, or inconsistent with the activity. Each category of behavior (save the neutral Look At) was defined to be characteristic of one of the activities, and each activity had at least one characteristic behavior pattern. A bout was defined as beginning with a characteristic behavior pattern and continuing as long as the succeeding behavior was consistent with the given activity. An inconsistent action terminated the current bout and initiated a new bout, based on the activity of which it was characteristic.

Activity definitions were derived both from functional considerations and from exploratory cluster analyses of the data set of frequencies of behavioral categories. Eating, for example, was characterized by Chew; it indicated consumption of food items of substantial size. Scraping was a less rewarding feeding pattern, characterized by Scrape and Hold Down with Foot, and Gleaning was less rewarding still, involving the use of Move Bill to pick up almost invisible particles of food. Excavation comprised the behavior used in unearthing new food resources, primarily Grasp, Pull, and Rummage. Searching involved slow, nonsocial locomotion, interspersed with Touch with Bill. Demolition was mainly concerned with tearing apart large, inedible objects, involving Grasp, Pull, and Pry. Transportation of food was characterized by Carry, Take, and Grab with Foot. Social activity was indicated by social behavior, such as Approach, Withdraw, Attack, or Threaten. Finally, Maintenance included Comfort movements and Bill Wipe.

The durations of all bouts of a given activity in a single session were summed and divided by the duration of the session to yield the proportion of time spent in each activity. The mean proportion across sessions was then computed for each bird, generating a data set with one measure for each of the nine activity classes for each focal individual. The analysis was then handled in the same fashion as the analysis of frequency. We used two-way analysis of variance for contrasts among the three older age classes, one-way analysis of data from the second field season for contrasts involving fledglings, and simple comparisons to locate the sources of significant main effects of age class.

The third data set was obtained by extracting the social interactions from each of the session transcripts. The criterion for the occurrence of a social interaction was an "initiation" event, consisting of either Approach, Attack, or Threaten performed by the focal animal or another individual, or of any behavior performed by another individual while the focal animal was watching. An interaction ended with a "termination" event, consisting either of Withdraw by either of the participants, or of any nonsocial behavior (e.g. Chew or Comfort) by the focal animal. Interactions involving no social behavior other than Look At were subsequently dropped from the analysis.

For each interaction, we recorded the age and sex of the two participants and indicated which of them was the "Initiator" and which the "Respondent". The first concern in the analysis was with the incidence of social interaction as a function of age class. We observed 1678

interactions in which at least one of the participants was an adult, 1061 interactions involving juveniles, 487 involving subadults, and 334 involving fledglings. The proportions of initiated interactions were compared using the G statistic (SOKAL & ROHLF 1981), while the distributions of interactions across recipient age classes were compared using χ^2 .

We were able to record the information about what the target individual was doing at the time it was approached for roughly 75% of the interactions we observed. As the final analysis of the incidence of interactions, we determined whether the choice of which animal to interact with was influenced by whether the potential recipient was actively feeding at the time, and whether the degree of influence of prior feeding on social initiations varied across age groups.

The content of the interaction was coded with a set of one/zero variables that indicated whether or not a particular social behavior was performed by a given participant. Behavior patterns tabulated included Approach, Threaten, Attack, Hunch, Carry, Take, and Withdraw. On the basis of these content variables, the outcome of the interaction was determined. There were five possibilities: Displacement, in which the initiator drives off the respondent; Theft, in which the initiator steals the resource from the respondent; Sequestering, in which the respondent carries away the resource; Defense, in which the respondent successfully drives off the initiator; and No Change, in which both animals end up feeding together. Affiliative interactions, in which the participants exhibited play or sexual behavior, did occur, particularly between fledglings or juveniles, but they were not included in this study. Differences in the distribution of behavioral contents and outcomes of social interactions across age class groupings were tested using χ^2 .

Results

Activity Budget

Because Eating and Searching together accounted for better than half of the total time budget (Fig. 1 A), the ratio of the two expresses, in a single measure, the relative "foraging efficiency" of the different age classes (Fig. 2).

Fledglings showed a lower foraging efficiency than other age classes (Fig. 2). Their proportion of time spent feeding was low, while their time spent searching was

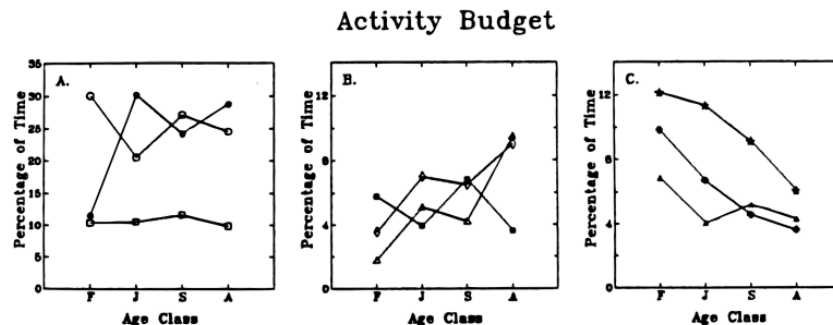


Fig. 1: Mean percentage of time spent in each of 9 activities for each age class. Values are - least-squares means, which correct for differences in sample size across field seasons. A) Major components: open circles = Search; filled circles = Eat; squares = Social. B) Minor components important in older individuals: triangles = Excavate; diamonds = Maintain; squares = Transport. C) Minor components important in younger individuals: stars = Scrape; crosses = Demolish; triangles = Glean.

relatively high (Fig. 1 A). They spent more of their time in demolition than any other age group ($p < 0.02$; Fig. 1C). Fledglings also devoted a relatively large portion of their time to scraping and gleaning (Fig. 1C) and little time to excavating new food resources (Fig. 1B). These findings are supported by the differences in frequency of the behavioral categories (Table 1). Fledglings performed eating movements less often (Chew: $p < 0.007$) and Touched ($p < 0.01$), Grasped ($p < 0.04$), and Scraped ($p = 0.05$) more often than other age classes.

Juveniles exhibited high foraging efficiencies (Fig. 2). In the 1988-89 field season, when food availability on the dump was high, juveniles spent nearly twice as much time in eating as they did in searching for food. Their foraging advantage over other age groups was maintained even in the second field season, when resources were leaner (Fig. 2). Juveniles were intermediate between subadults and fledglings for most of the minor components of the activity budget (Figs. 1B, 1C).

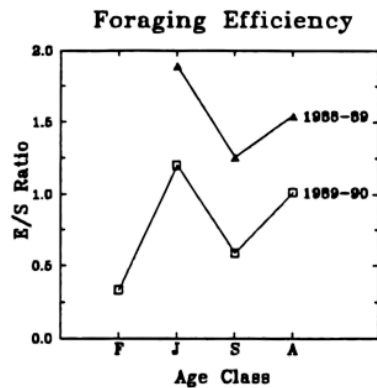


Fig. 2: Mean foraging efficiency, as the ratio of time spent eating to time spent searching, for each age group. Data from the two field seasons are plotted separately.

The amount of time that juveniles spent feeding was as high as that of adults, however, even though they invested less time in searching than any other age group (Fig. 1A).

Subadults, in contrast, spent more of their time searching than did juveniles ($p < 0.04$; Fig. 1A) and less time feeding. Their resulting foraging efficiency ratio was less than that of juveniles (Fig. 2). This is supported by the frequency data (Table 1): subadults exhibited a significantly lower frequency of eating (Chew: $p < 0.05$) than other age classes. Subadults also spent a larger proportion of their time transporting food items than did either adults or juveniles ($p < 0.03$; Fig. 1B). Adults spent more of their time excavating new food resources than the younger animals did ($p = 0.05$; Fig. 1B) and they exhibited significantly higher frequencies of Rummage ($p < 0.04$), Grasp ($p < 0.03$) and Pull ($p < 0.03$) than did other age groups (Table 1).

Social Interactions

Incidence: The proportion of time spent in social activity was virtually constant across age classes (Fig. 1A) at about 10 % of the total activity budget. The frequency of interactions also did not differ significantly between age classes, averaging about 8 per 10-min observation session.

Adults and juveniles differed from other age classes in the number of interactions they initiated: Of all interactions in which at least one of the participants was an adult, the adult initiated the encounter 51.6% of the time ($p < 0.05$). The *Table 1*: Mean frequency of behavior per session by age class. Means are least-squares means, which correct for differences in sample size across field seasons. Means that are significantly higher than at least one of the three alternatives are marked with an asterisk; those that are significantly lower are marked with a dagger.

Age class	Foraging behavior				
	Chew	Move Bill	Touch	Bill Hold	Scrape
A	24.3 *	5.94	7.13	2.98 †	4.03
S	19.3 †	6.61	6.72	4.35	5.55
J	21.0	4.96	7.73	3.79	8.16 *
F	3.9 †	7.70	9.59 *	4.85	8.17 *
	Pry	Dig	Probe	Grasp	Pull
A	0.65	0.03	0.49	4.96 *	4.99 *
S	1.04	0.17	0.78	3.73	2.67
J	0.60	0.17	0.75	3.80	3.70
F	0.85	0.03	0.30	5.45 *	4.74 *
	Rummage	Carry	Foot Grab	Hold Down	Take
A	5.91*	2.16	0.91	1.59	0.26
S	2.78	2.61	1.00	2.18	0.46
J	3.30	1.50	0.60	2.35	0.37
F	1.35	0.66 †	0.76	2.51	0.13
	Social and other behavior				
	Attack	Threaten	Hunch	Bill Wipe	Comfort
A	0.35	0.48	0.17	2.94	2.00
S	0.21	0.34	0.02	1.87	4.09 *
J	0.91 *	0.84	0.90 *	1.93	2.96
F	0.72	0.30	0.28	0.80	1.75

proportion for juveniles was more striking: juveniles initiated 54.2% of the interactions in which they were involved ($p < 0.005$). Subadults and fledglings, on the other hand, were more often recipients than initiators of interaction. Subadults initiated 42.6% of their interactions ($p < 0.001$), and fledglings initiated 40.3 % of theirs ($p < 0.001$).

A higher proportion of the interactions initiated by juveniles were also directed to adults than was the case for interactions initiated by subadults (59.9% vs. 45.8%; $p < 0.001$). In fact, the propensity of juveniles to approach adults was larger than the

tendency of adults to approach one another (59.9% vs. 54.5%; $p < 0.04$). Fledglings, on the other hand, primarily chose to interact with other fledglings. Over half of the interactions initiated by fledglings were directed to other fledglings, which was far in excess of the frequency with which fledglings were approached by the other age groups (50.9% vs. 20.4%; $p < 0.001$).

To display the effect of prior behavior, we plotted the proportion of recipients that were feeding before the interaction began for each age class of initiators (Fig. 3). In both field seasons, subadults were more likely than the other age groups to approach another animal that was actively feeding (1988-89: $p < 0.03$; 1989-90: $p < 0.001$).

Approaches to Feeding Birds

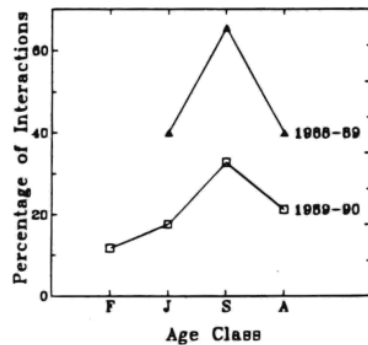


Fig. 3: Percentage of social interactions in which the respondent was known to be feeding at the time the interaction began, by age class of initiator. Data from the two field seasons are plotted separately

Content: Agonistic behavior in the kea was analyzed in terms of the proportion of interactions that included a particular behavior pattern, as a function of the age classes of the participants. These values are plotted separately by age class of "actor" and "recipient" of the behavior for Attack, Threaten and Hunch (Fig. 4).

Fledglings were far more likely to be attacked than were any other age group ($p < 0.001$; Fig. 4 A). They were also more likely to initiate an attack themselves ($p < 0.001$; Fig. 4 A). Of the three older age classes, subadults were more likely to be attacked than to attack other animals themselves ($p < 0.001$; Fig. 4 A), while adults and juveniles showed comparable rates of giving and receiving attacks (Fig. 4 A). Fledglings were less likely to be threatened than the other age groups ($p < 0.001$; Fig. 4 B), but there were no significant differences among age groups in the incidence of threatening other individuals (Fig. 4 B).

The age class effect on the incidence of hunch displays was substantial. Most hunches were performed by juveniles ($p < 0.001$; Fig. 4 C); over all interactions involving hunching, 83 % were by juveniles (see also age differences in the raw frequency of Hunch: Table 1, $p < 0.0005$). Fledglings also performed the behavior, though at a reduced frequency. Hunches were virtually never observed in subadults or adults (Fig. 4 C). The majority of hunches, however, were directed to adults ($p < 0.001$; Fig. 4 C). Hunches to subadults occurred at about half the relative frequency of those to adults.

Outcomes of Hunching: In juveniles, hunching had a significant impact on the likelihood of their obtaining food. Juveniles that approached adults in a hunch (Table 2 A) did not displace the adult more often, but they were more often tolerated and

allowed to feed nearby ($p < 0.03$). Juveniles that hunched in response to an adult's approach (Table 2 B) were displaced significantly less often ($p < 0.001$) and were more often allowed to remain feeding ($p < 0.001$).

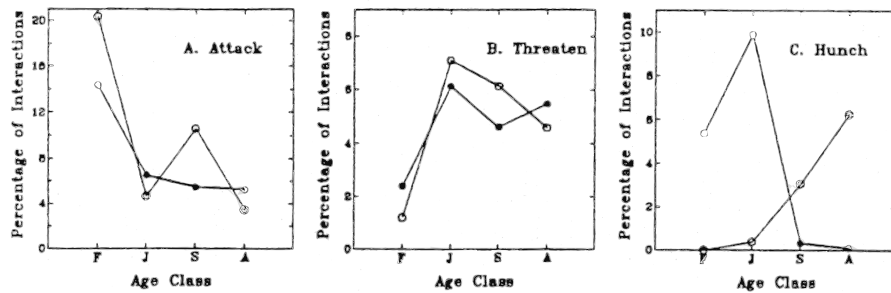


Fig. 4: Percentage of social interactions that involved each of three categories of agonistic behavior; filled circles: by age class of actor, open circles: by age class of recipient.

The hunch display was only the most visible sign of the special status of juveniles, however. Even when all interactions involving hunching were removed from the data set, juveniles still retained a considerable advantage over subadults and fledglings in their interactions with adults. Non-hunching juveniles were displaced by approaching adults 68.9 % of the time, in contrast to 74.1 % for fledglings and 84.1 % for subadults ($p < 0.001$; Fig. 5 A). They were allowed to remain feeding 14.8 % of the time, in contrast to 5.6 % for fledglings and 1.9 % for subadults ($p < 0.001$). The same pattern held true when the younger bird initiated the interaction: nonhunching juveniles successfully displaced adults 35.5 % of the time, while this was true for 26.3 % of approaches by fledglings and 16.0 % of those by subadults ($p < 0.001$; Fig. 5 A). In addition, adults defended their resource 22.2 % of the time against approaching fledglings and 26.5 % of the time against subadults, while the figure for nonhunching juveniles was 10.0 % ($p < 0.001$; Fig. 5 B).

Other Outcomes: Overall, most social interactions resulted in displacement of the recipient animal, no matter which age classes were involved (Fig. 5 A), possibly reflecting the fact that the recipient commonly held no resource worth defending. Adults generally displaced subadults more readily than they did juveniles ($p < 0.0001$; Fig. 5 A). Juveniles showed a similar pattern: they also displaced subadults more readily than they did either adults or other juveniles ($p < 0.02$; Fig. 5 A). Subadults, on the other hand, were less likely to displace adults than were juveniles or even fledglings ($p < 0.001$; Fig. 5 A). Successful defense of food resources also differed significantly, depending on the age of the initiating animal (Fig. 5 B). All age categories defended more readily against subadults than against any other age group ($p < 0.001$; Fig. 5 B).

Theft and sequestering also demonstrated strong age-dependent influences (Fig. 6). Subadults stole food more often than other age classes ($p < 0.004$; Fig. 6 A) and they carried their food away more often ($p < 0.003$; Fig. 6 B). All three of the older age groups carried food away more often when approached by juveniles than when approached by either subadults or adults ($p < 0.001$; Fig. 6 B).

Table 2: Consequences of juvenile hunch display in adult/juvenile interactions (A. initiated by juvenile, B. by adult). Outcomes that were significantly increased or decreased in probability as a consequence of hunching are marked with an asterisk.

Display		Outcome (% of interactions)			Sample size
		Juvenile withdraws	Share resource	Adult withdraws	
A.	Hunch	10.0	28.3*	51.7	60
	No hunch	11.1	15.4	55.0	298
B.	Hunch	27.6*	48.3*	13.8	29
	No hunch	68.9	14.8	9.3	270

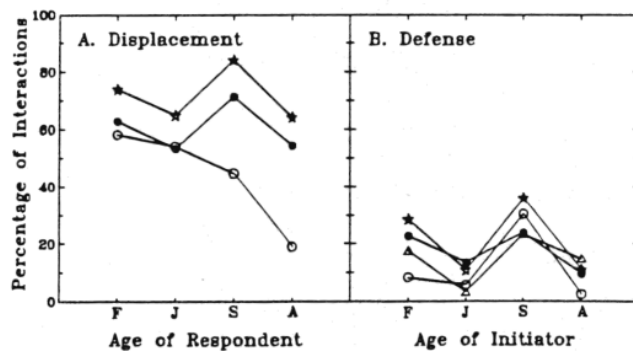


Fig. 5: Major outcomes of social interaction. A) Percentage of interactions in which the initiator successfully displaced the respondent, by age of respondent. Symbols indicate age class of initiator: stars = adults; open circles = subadults; filled circles = juveniles. The frequency of interactions initiated by fledglings

was too low to plot reliably. B) Percentage of interactions in which the respondent drove off the initiator, by age of initiator. Symbols indicate age class of respondent: stars = adults; open circles = subadults; filled circles = juveniles; triangles = fledglings.

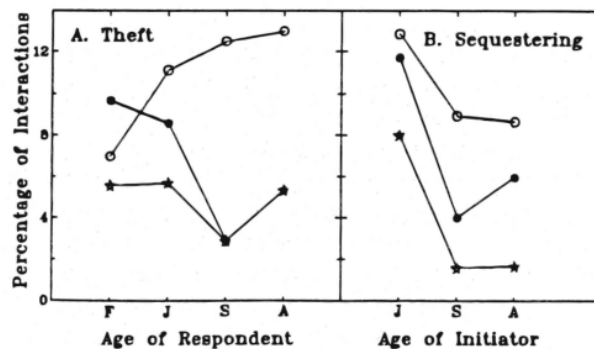


Fig. 6: Minor outcomes of social interaction. A) Percentage of interactions in which the initiator stole the resource from the respondent, by age of respondent. Symbols indicate age class of initiator: stars = adults; open circles = subadults; filled circles = juveniles. B) Percentage of interactions in which the respondent retained the resource by carrying it

away from the initiator, by age of initiator. Symbols indicate age class of respondent (see A). The frequency of both of these outcomes for interactions involving fledglings was too low to plot reliably

Discussion

Each of the four age classes of kea shows distinctive patterns of foraging behavior, patterns that are shaped by social abilities and status, as well as by foraging expertise.

Fledglings

Fledgling kea are poor at unearthing new food resources (Table 1; Fig. 1 B), and they eat relatively little on their own (Fig. 1 A). Fledglings show little evidence of an ability to discriminate edible items. Even when other animals are actively feeding, fledglings spend much of their time manipulating inedible objects (Fig. 1 C). This phenomenon is not restricted to kea: the young of various species are known to manipulate otherwise inappropriate objects (HIGUCHI 1986; FICKEN 1977; SKUTCH 1976).

The low proficiency of fledgling keas does not mean that they go without food, however. Kea have extended post-fledging care (JACKSON 1962, 1963): We have observed adult males to regurgitate to fledglings for up to a month after they leave the nest. The extensive social interactions of fledglings are relatively indiscriminate with respect to foraging. Fledglings generally do not approach foraging animals to obtain resources from them (Fig. 3). The social interactions of fledglings are more aggressive than those of other age groups (Fig. 4 A), and many of these aggressive interactions occur in the context of social play (KELLER 1975; CAMPBELL 1976). Such play bouts can be intensive, lasting up to 1 h and including as many as five individuals of both sexes.

Juveniles

Juvenile kea are the most efficient foragers of any age class (Fig. 2), largely because they are more effective at obtaining their food by social means. They initiate more interactions with adults than other age classes and are more successful at keeping the resources they obtain (Fig. 5 A, B).

One social behavior used by juveniles to obtain food is hunching. When juveniles hunch, they are more likely to gain access to new resources, and they are less likely to be displaced from the ones they already hold (Table 2). When confronted by juveniles, other animals either give up their resource (Fig. 5 A) or carry it away (Fig. 6 B). Although juveniles hunch more often to adults, they also hunch to subadults and rarely to other juveniles (Fig. 4 C). They do not appear to hunch only to specific individuals: One juvenile was observed to hunch to three different adults and two different sub-adults. Fledglings also display the hunch behavior, but at a lower frequency than juveniles (Table 1; Fig. 4 C).

Hunching in kea appears to serve as an appeasement display, in that it reduces the likelihood of aggression by adults (Table 2). Such juvenile appeasement displays are known in other species of birds. According to TINBERGEN (1960) and DRURY & SMITH (1968), juvenile herring gulls can inhibit adult aggression by a display also referred to as "hunching." Although it does not appear to be mediated by appeasement,

a similarly favored social status for juveniles has also been recorded in several species of corvids (LOCKIE 1956; BROWN 1963; BALDA & BALDA 1978; BROWN & BROWN 1984; BARKAN et al. 1986).

Subadults

Subadults are less efficient at foraging than are juveniles (Fig. 1 A; Fig. 2). They do not exhibit the hunch displays that juveniles use to obtain access to food found by adults (Fig. 4 C). The loss in subadults of the characteristic juvenile color pattern may render the hunch display less effective. They also do not display behavior patterns, such as Rummage, that are used principally by adults to uncover new resources (Table 1).

Subadults are also less capable of protecting resources once they have found them. They have low social status and are readily displaced by some juveniles and virtually all adults (Fig. 5 A). These observations contrast strongly with published studies of the ontogeny of foraging in water birds, in which foraging efficiency has generally been found to increase monotonically with age (e.g. MACLEAN 1986). Subadults make extensive use of theft as a foraging strategy. In contrast to younger animals, subadults principally approach birds that are already feeding (Fig. 3), and they steal more and carry food away more than other age groups (Figs. 6 A, B). In spite of the use of theft, however, subadults do not obtain as much food as adults or juveniles. Subadults probably have recourse to kleptoparasitism mainly to compensate for a loss of the ability to obtain food by other social means.

BROCKMANN & BARNARD (1976) reported that kleptoparasitism has not been observed in Psittaciformes. Kleptoparasitism is, however, common in kea and particularly so in subadults. The relationship of age class to the incidence and success of piracy varies in other species, even in seabirds, where kleptoparasitism is a favored foraging technique. Juvenile herring gulls have been observed to steal more food than adults, but the reverse was true of laughing gulls (BURGER & GOCHFELD 1981). In the kelp gull, kleptoparasitism decreased with age, while the efficiency of foraging behavior increased (HOCKEY et al. 1989). BURGER & GOCHFELD (1979) found that although subadult ring-billed gulls engaged in more attempts to steal, they were less successful than adults.

Adults

Adult kea are capable scavengers, particularly with respect to the discovery and exploitation of new resources (Table 1, Fig. 1 B). They waste little time in manipulating unprofitable items (Fig. 1 C) and show considerable skill in identifying and uncovering food. In spite of the fact that adults are more proficient at foraging, however, they are not more efficient, in terms of the ratio of eating time to searching time, than juveniles (Fig. 2). The difference is that juvenile foraging efficiency is maintained by social behavior, while adult efficiency is maintained by foraging skill.

Conclusions

The development of foraging ability in the kea appears to be influenced as much by social factors as by individual experience. Fledglings begin independent life

manipulating and demolishing anything within reach. They interact sparingly with adult kea, other than those that regurgitate to them directly. Juveniles are much more socially oriented, and they frequently approach adults, from whom they may obtain indirect access to food. Juveniles do not, however, discriminate in their approaches between an animal that is eating and one that is not.

Subadults, in contrast, are highly selective in their social interactions, approaching mainly individuals that are currently in possession of valuable, vulnerable resources. The development of foraging can thus be seen as a transition from relatively nonsocial and indiscriminate exploring, to focused social interaction with adults, to attending mainly to the objects that adults control, and finally to focusing attention on the objects themselves.

A copious literature has accumulated, demonstrating that juvenile birds are less successful at foraging than adults (ASHMOLE & TOVAR 1968; reviewed in BURGER 1988). As our observations of kea illustrate, however, the maturation of foraging ability is not necessarily a simple, monotonic process. Foraging in highly social species occurs within a larger context of the social role of the individual. Its maturation is influenced and constrained by social factors in different ways during successive developmental stages.

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Appendix: Ethogram of Object-related Behavior in the Kea

Move Bill (KELLER 1976 = Schnabelspitzendrücken). A forceps-like movement of the bill, opposing the tips of the mandible and maxilla, often accompanied by in-and-out movements of the tongue. Commonly associated with preening, but also occurs in the manipulation of small food items, such as ants or bread crumbs.

Chew (KELLER 1976 = Kauen). An object is held against the palate with the tongue. The mandible is then repeatedly pressed against it, reducing the material to a pulp. KELLER (1976) noted that this technique is used with most large food items, including lettuce, carrots, fruits, and meat.

Touch with Bill. A stationary object on the ground is briefly touched with the tip of the maxilla.

Grab with Foot (POTTS 1969). An object is grasped with a foot and held up to the bill to be Chewed or otherwise manipulated. SMITH (1971) referred to this as "prehensile-footed" feeding. KELLER (1976) described kea squatting on one foot while holding an object with the free foot, surrounding it by all four toes. We observed this behavior when the birds were feeding on small items, as well as during foraging in beech trees (*Nothofagus* sp.), where a cluster of leaves or a branch is grasped with the foot and held close to the bill.

Hold Down with Foot (POTTS 1969). An object is held against the substrate with a foot while the bird manipulates it with the bill. SMITH (1971) referred to this as "tether-footed" feeding. POTTS (1969) observed this to be less common than Grab with Foot, but our observations suggest that the choice of behavior depends on the nature of the food item and the type of feeding technique involved. Hold Down is strongly associated with Scrape and Pull, while Grab is associated with Chew.

Hold in Bill. A small object is held in the bill while the animal is stationary. The object may be manipulated, rotated, briefly chewed or held without manipulation. This includes BREJAART's (1988) description of kea rolling grasshoppers with their tongue. Hold in Bill typically does not involve actual feeding, although it may precede it.

Take Object from (JACKSON 1963). A kea seizes, or attempts to seize, an object with its bill that is currently being held by another bird. This is often followed by Carry. JACKSON (1963) observed fledglings to steal tidbits from each other in this manner.

Carry (KELLER 1976 = Tragen). An object is transported, typically by carrying it in the bill while the bird runs or walks away. We observed several instances in which an object was carried in the feet while the kea flew a short distance. Often associated with Take.

Scrape (POTTS 1969). An object is held in position with the maxilla while the mandible is scraped over the surface of the object, removing bits of material into the mouth (POTTS 1969). Scrape is often accompanied by Hold Down with Foot. Scrape includes one form of the behavior that KELLER (1976) termed Entrinden, in which the maxilla is hooked onto an object. The mandible is then placed a small distance away and is drawn against the maxilla, lifting small pieces off the surface. ZEIGLER (1975) describes fruit and greens being impaled on the maxilla, while the mandible is moved up and down in a rasping, scraping movement. BREJAART (1988) observed kea to scrape off the leaves from mountain daisy (*Celmisia* sp.) in this fashion.

Pry. Pry refers to KELLER's (1976) second form of Entrinden, in which the maxilla is drawn over a surface. When the tip catches in a crevice, the maxilla is pulled and twisted to widen the opening and break off pieces of the object. In contrast to Pull and Tear, the force in Prying is exerted mainly with the head and neck. The tip of the mandible may be used as a fulcrum, or the bird may pry against the curved upper surface of the maxilla or twist the maxilla laterally.

Grasp with Bill. A large or anchored object is grasped with the bill. This behavior is often associated with Pull or Pry.

Pull and Tear. Once an object is grasped in the bill, the kea exerts leverage through the back and legs, pulling toward itself. Both feet are planted on the ground, with the hallux flexed and serving as a fulcrum, with the result that parts of an object are separated, torn, or pulled toward the bird.

Dig/Rake (KELLER 1976 = Graben). The bill is inserted into the soil and then pulled out, bringing with it soil, leaves or other items. KELLER (1976) considered Raking, in which dirt is pushed to one side of a hole, a graded version of Rummage (Fortschleudern). We believe that it is more closely related to Dig. Similarly, we include in this category KELLER's (1976) Pflugen, in which the kea moves backward while digging with its bill set in the ground, resulting in the production of a small

trench. CAMPBELL (1976) reported that kea use Dig to obtain roots of the mountain daisy (*Celmisia* sp.), and BREJAART (1988) observed kea to find insects in this manner.

Probe. The maxilla is inserted into crevices in wood or among rocks. The bird may stand on a rock and work the bill into crevices all the way around it, or it may drag the bill along a crack in a continuous motion for several cm.

Rummage. According to KELLER (1976), an object is picked up with the bill and let go with a quick lateral movement of the head, so that the item is flung for some distance. We observed kea in the field repeatedly to grasp objects with their bills and throw them aside; small objects may be thrown more than a meter. This behavior is used to remove unwanted objects from a pile in an effort to uncover other items. It differs from Toss Up, in that the movement of the head is always sideways, resulting in a lateral throw, and from KELLER's (1976) more general description of Fortschleudern in that it does not include simply moving objects aside.

Toss Up (POTTS 1969). While an object is held in the bill, the head is jerked vertically, tossing the object into the air. The behavior may be accompanied by a Hop or Wing Flap just before the object is released and may be repeated for several min at a time. POTTS (1969) observed young birds repeatedly to Toss Up the end of a broom stick, and we observed this action in kea attempting to open walnut shells. Juveniles Toss Up rocks and other small objects as a component of social interaction, including play. We also observed this behavior during inter-actions, possibly courtship, between adults of opposite sexes.

Drink. According to POTTS (1969), the partially open bill is dipped into the water and the tongue is moved quickly in and out, lapping water in a manner similar to that described by DILGER (1960) for *Agapornis*. Head shaking generally follows drinking. KELLER (1976) distinguished this behavior from Schopfendes Trinken, in which the water is ladled with the mandible and swallowed by lifting the head. On warm days, we observed kea to soak dry food in water before eating it. KELLER (1976) observed this to occur in some captive groups of kea, but not in others, and concluded that it may result from tradition. Kea also eat snow and ice and lap dew (KELLER 1976).

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